Soil in the ecosystem

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SUMMARY

1 The paper briefly reviews the significance of interactions between above- and below-ground biotic processes and biota in terrestrial ecosystems. It demonstrates the essential connectedness of terrestrial ecosystems, and the artificiality of separating ecosystems into soil and above-ground components.

2 The often great spatial and temporal variability of soil properties is discussed, and some of the causes analysed. Changes in labile soil propeties with time caused by *Betula pendula* are noted in more detail.

3 The other main subjects used as illustrations are: differences in death rates of buried seed populations; the significance of seed dispersal by ants; the role of rotting wood as a niche for seedling establishment; root competition; ectomycorrhizal successions associated with ageing trees; the effects of herbivores on soil processes.

4 It is concluded that the functional interactions of ecosystems are transient rather than fixed. The variability and dynamic nature of soil properties should always be borne in mind by soil biologists and ecologists.

INTRODUCTION

For this paper, I was asked to assess '. . . the significance of the biotic processes in the soil environment in relation to processes in the whole ecosystem, particularly emphasizing dynamic aspects.' Fortunately, editorial fiat solves the problem of where to strike the balance between monographic treatment and the single sentence summary, e.g. terrestrial ecosystems are always changing in time and cannot exist without soil (excluding soil-less 'micro-ecosystems', such as those of rock and bark). Accordingly, I shall briefly examine first the functional connectedness of ecosystems, and second, the variability of soil in space and time. Finally, I shall discuss a limited number of interactions between the above- and below-ground systems, choosing examples which interest me but which are poorly understood.

ECOSYSTEM CONNECTEDNESS

It is trite, but none the less true, to state that soils and soil biotic processes are an essential part of terrestrial ecosystems. Micro-organisms fix much, if not most, of the nitrogen made available to plants, and speed up the weathering of essential elements from soil minerals. Plant nutrients, critically nitrogen and phosphorus, are

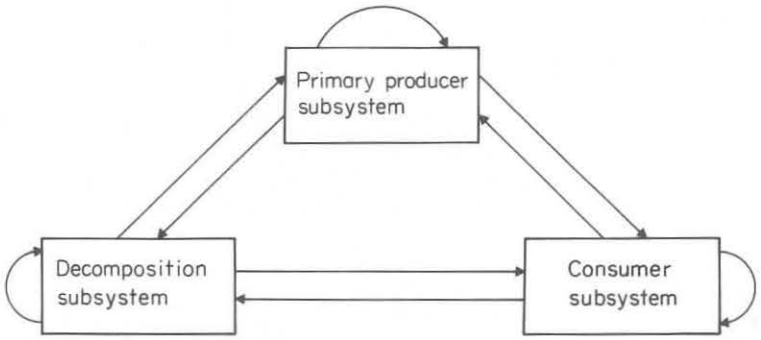

FIG. 1. Simple three-compartment model of ecosystem structure and internal links (after Swift, Heal & Anderson 1979; Andersen, MacMahon & Wolfe 1980; MacMahon 1981).

largely recirculated via decomposition of organic matter by micro-organisms. (Some plant-available, or at least ectomycorrhizal-available, soluble organic N and P may be produced from faunal feeding, and even directly from autolysis in dying tissues.) Mycorrhizas help most vascular plant taxa to tap scarce N and P. The soil fauna *inter alia* facilitates decomposition by comminuting organic remains, is preyed upon by many vertebrates, and helps to maintain soil as a well aerated rooting medium.

The simplest conceptual view of an ecosystem that is still useful, is as a three-compartment model (Fig. 1). This omits exchanges with and influences of the atmosphere, lithosphere, and other ecosystems, but otherwise neatly summarizes the internal connectedness of terrestrial ecosystems, showing the major routes of transfer of matter and/or interactions. The consumer and decomposer compartments or subsystems can be subdivided in terms of food webs; the organic detritus part of the consumer subsystems can be described as a network of molecular changes, of catabolic transformations and humus synthesis. Figure 2 is a limited expansion of this simple model. The consumer and decomposer compartments are arbitrarily divided into six and two compartments respectively. Links with the atmosphere and other ecosystems are still omitted, and also *inter alia* compartments with animal and microbial pathogens, and interactions within compartments (e.g. competition and interference between organisms, nutrient and carbon fluxes within plants, synthesis of humus polymers). The main subject material of this volume falls within five compartments: decomposers, saprovores, below-ground predators, root grazers, and plants and their associated mycorrhizas.

There are two main drawbacks to the expanded model of trophic relationships, apart from its generalization and lack of quantification. First, to avoid excessive expansion of the model, all but one of the defined compartments fall both above and below ground. One problem is that individuals of some species occur above and below ground at different stages of their life histories, e.g. many insects with winged adults have root-feeding larvae. Other species regularly commute between the soil and the surface even at the same life-history stages, e.g. the common earthworm

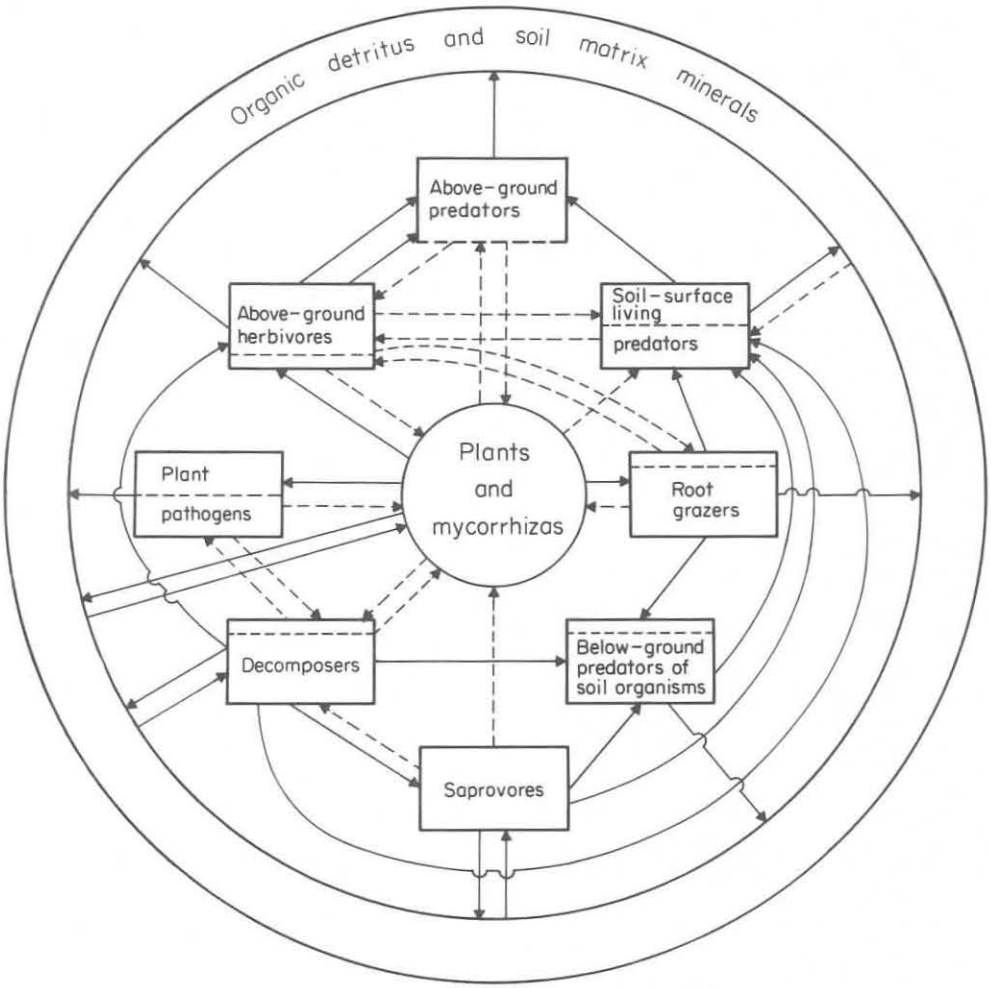

FIG. 2. Ten-compartment model of ecosystem structure. The relative importance above and below ground of organism compartments is shown by horizontal dashed lines. Dashed arrows show interactions not involving significant transfers of matter; continuous arrows show major routes of transfer of matter. Interactions coinciding with matter transfer routes are not shown separately.

Lumbricus terrestris, and most British ants. Second, many organisms have a degree of trophic flexibility such that they must be classified under more than one compartment. The honey fungus, *Armillaria mellea*, forms mycorrhizas with orchids, is a common saprophyte, but is a virulent pathogen of trees and many woody and herbaceous plants (Ramsbottom 1953; Mosse 1978). Blackbirds (*Turdus merula*) and many other birds eat a variety of invertebrates and of fruits. Badgers (*Meles meles*) depend mostly on earthworms in parts of north-west Europe, but also eat leaves, seeds, fruits, roots, fungal fruit-bodies, rodents, amphibians, rabbits (*Oryctolagus cuniculus*), insects and carrion (Kruuk & Parish 1981). They therefore feed,

at least to some extent, within eight of the nine producer/consumer/decomposer boxes in Fig. 2 and, as it is likely that the occasional item of plant material infected with rust, smut or mildew will be ingested, they probably feed within all compartments! This, of course, highlights the artificiality of attempts to compress complex systems into simple models.

However, despite its limitations, Fig. 2 shows that all the predominantly below-ground compartments are linked to mainly above-ground compartments. Indeed, even at this simple, ten-compartment level, there is a web of both influences and of routes of transfer of material. This means that an impact on one compartment is likely to reverberate across the web. For example, direct addition of inorganic fertilizer influences decomposition (Swift, Heal & Anderson 1979), plant production, and the biomass and species richness of arthropod, herbivore and carnivore populations (Hurd *et al.* 1971; Hurd & Wolf 1974). No increase in small herbivorous mammals was detected in the latter study, but no other consumer groups were examined. Detailed word models can be formulated to indicate the likely extent of such repercussions. Swift *et al.* (1979) indicate how a reduction in grazing on a temperate grassland could cause a sequence of changes within the decomposer subsystem leading either to increased or reduced N availability to plants, depending on soil moisture status. Changed N availability would lead to changed N uptake by plants and possibly to eventual changes in species composition of the sward. Either could result in grazing pressures further changing with voluntary grazing. When the interactions have been quantified, mathematical models can be used to predict the degree of change (Innis 1978).

Many interactions within ecosystems do not involve transfers of significant quantities of matter, e.g. chemical interference, seed and spore dispersal. Chemical interference seems to be widespread. Apart from allelopathic (plant against plant) phenomena, plants influence micro-organisms and vice versa. The ectomycorrhizas of certain conifers are inhibited by *Cladonia* spp. (Brown & Mikola 1974; Fisher 1979a) and *Calluna vulgaris* (Weatherell 1953; Handley 1963). Seeds produce an array of chemicals that inhibit various micro-organisms (Nickell 1959). This may account for the persistence of soil seed banks; without such inhibitors, most seeds might quickly rot after dispersal unless they germinated (Rice 1979; Fisher 1979b). Soil micro-organisms in turn produce chemicals that inhibit germination (Lynch 1978; Kirkpatrick & Bazzaz 1979) and subsequent plant growth (Chapman & Lynch 1983). However, micro-organisms can also promote germination under some circumstances (Abdulla 1970; Leeuwen 1981). The mechanism of this is unknown, but is presumably by the micro-organisms either producing germination-promoting chemicals, or breaking down the fruit or seed coat. There are also reports of micro-organisms producing growth-promoting auxins (Valadon & Lodge 1970; Tinker 1980), but the significance, if any, of these to plants in the field, is unknown.

Perhaps the most tangible form of internal link within most terrestrial ecosystems is not shown in Fig. 2. This is that the vascular plant components may commonly if not generally be physically linked through root grafts (Sutton 1969) and interconnections between mycorrhizal hyphae (Heap & Newman 1980; Brownlee

et al. 1983). These phenomena and their physiological implications have not been widely and systematically investigated. However, Brownlee *et al.* (1983) and Read, Francis & Finlay (p. 193) have shown that ^{14}C-labelled assimilate is distributed via interplant mycorrhizal connections. Further, Stone (1974) demonstrated that when *Pinus resinosa* trees were girdled (which prevents transport of photosynthate to root systems), individuals with intact neighbours could survive for at least 18 years. In one instance, a whole stand was maintained by only two-thirds of the trees. Although the girdled trees did not grow as well as ungirdled ones, Stone concluded that: '. . . there are grounds for considering the entire stand root system as unitary and communal at least with respect to phloem transport.'

The ten-compartment model, or any variation or development of it, would clearly be much more useful if the compartments, transfers of material, and other interactions, could be quantified for a range of contrasting ecosystems. The compartments and transfers can be characterized by pools and flows of different elements. However, while this can now be approximated above ground for many ecosystems, there are too many gaps in the literature to permit a comprehensive approximation below-ground in any ecosystem. There are many estimates of the population size and/or biomass of particular taxonomic and functional groups of soil animals and micro-organisms, but far fewer data on turnover times (i.e. inputs to the dead organic pool) and on the functional relationships between different groups. Root grazers are one functional group whose activities are particularly poorly understood.

The model could also be characterized by an organism population approach. This would certainly be needed to quantify many of the interactions not involving substantial transfer of material, e.g. chemical inhibition or promotion of germination of or micro-organism activity. More compartments would need to be recognized, but the immediate difficulty is that for so many groups the basic problems of recognition and taxonomy are unresolved, far less those of understanding their biology and ecology.

SOIL VARIABILITY

Apart from the intrinsic complexity of soils, physical and chemical as well as biotic, their spatial and temporal variability is a further major barrier against understanding their ecology. Jenny's explanations (1941, 1980) of how soil varies with differences in state factors (the 'clorpt' equation) are well known, and provide the conceptual framework for studying soil multiformity. However, there seems to be less awareness of the scales and intricacy of soil variability.

Spatial variability

The often great variation in vegetation composition from point to point is unconcealed, if not always recognized. That soils also characteristically show great variability in space (Beckett & Webster 1971) is less evident. Variation is often on a scale so small that a single tree can be rooted in two or more quite different soils (Lyford 1974). Soil can vary abruptly in drainage and mineralogical composition.

This is particularly likely in transported materials, such as the glacial drifts commonly occurring in the British uplands (Robinson & Lloyd 1915; Kantey & Morse 1965). Differences in past land-use can also cause persistent differences in many soil properties (Van Goor 1954; Armson 1959).

Temporal variability

Many soil properties change appreciably only over long periods of time, e.g. the degree of overall mineral weathering, particular-size distribution. Other properties vary measurably during the usually shorter time-spans of secondary succession and the lives of individual plants. Different plant species can vary greatly in levels of nutrient and secondary chemical composition, and also in the extent to which they modify the chemical composition of rain dripping off their leaves and canalized as stemflow. Thus, when an individual of one species or a patch of vegetation is replaced by one different, changes in humus form and quantity, and in plant-influenced properties such as pH and exchangeable base content, must be expected. Changes in such properties occur as gradients radially from main stems and with depth (Zinke 1962; Grubb, Green & Merrifield 1969; Gersper & Holowaychuck

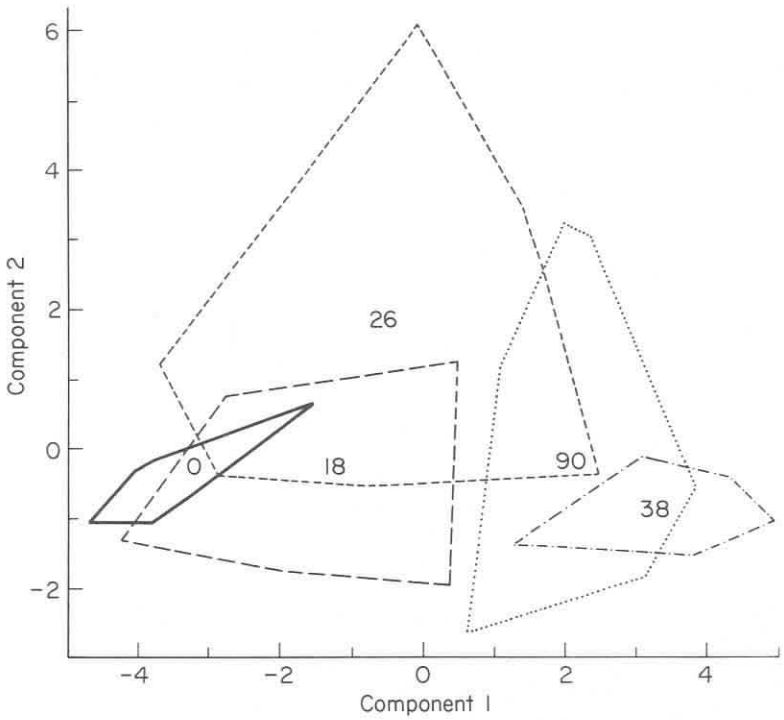

FIG. 3. Summary of changes in soil A and B horizons under a successional age sequence of *Betula pendula* stands near Advie, Morayshire: mean and range (n = 9) for each age-class of values of the first two components from principal component analysis of labile profile characteristics (see Fig. 4).

1970a, b). They are characteristically reversible. Page (1968, 1974) showed that surface acidity and the depth of surface organic matter accumulations varied cyclically during the life of many conifer species, the first declining and then increasing, and the second showing a contrasting trend.

I have studied, and summarized elsewhere, the changes in soil 'chemical' properties that occur when birch colonizes *Calluna vulgaris*-dominated moorland (Miles & Young 1980). These include increases in pH, exchangeable calcium, total phosphorus, and rates of nitrogen mineralization and cellulose decomposition. The appearance and structure of the soils change also. Figures 3 and 4 show the distribution and composition of the first two components from principal component analysis of labile, non-chemical properties across a site with a successional gradient from *C. vulgaris* to 91-year-old *B. pendula*. There is a clear trend in the first component, representing in particular a reduction in the number of horizons, in H horizon depth and, in the A horizon, increases in root and organic matter content, and in porosity and crumb structure. These changes, and those in colour, reflect the pronounced increase in microbial and faunal activity in the topsoil along the birch age gradient. Earthworm populations increased dramatically (Fig. 5). Figures 3 and 5 show, analogously to Page's (1968, 1974) findings under conifers, that the soil

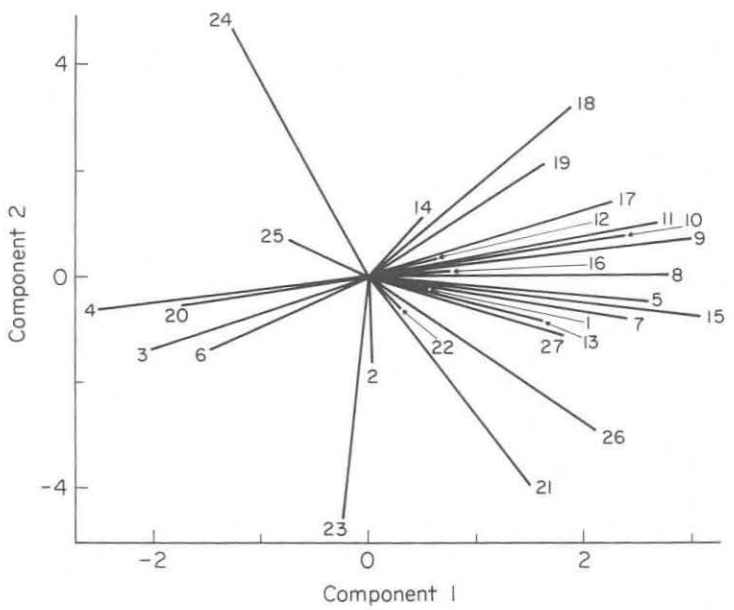

FIG. 4. Eigen vector diagram showing the coefficients of the linear function defining the two components in Fig. 3 These indicate the weighting to be placed on each soil characteristic in interpreting Fig. 3 (1–3, thickness of L, F and H horizons; 4, total number of horizons; 5–16, A horizon parameters; 5–7 colour—hue, value and chroma (Munsell scores); 8, % organic matter; 9, porosity; 10–11, structure strength and shape; 12, consistency; 13–14, sharpness; 17–26, B horizon parameters, as for parameters 5–14 in the A horizon; 27, B horizon cementation.

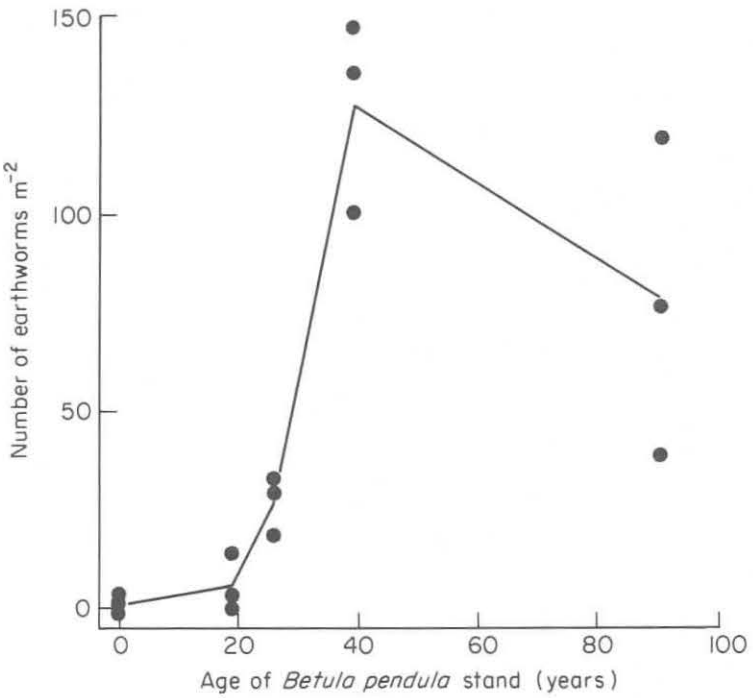

FIG. 5. Changes in total earthworm populations (number m^{-2} sampled by formaldehyde method) under the successional age sequence of *Betula pendula* stands in Fig. 5.

changes tended to reverse under very old birch, when the stand was opening up with tree senescence and death, and *C. vulgaris* was reinvading locally.

The vegetation reacts to these early soil changes, with the field layer gradually changing to one more characteristic of upland birchwoods, and increasing in species diversity. The soil changes are probably 'driven' mainly by the increased pH, with consequent effects on the vegetation. Figure 6 shows the positive correlation over all the successional stands I have studied between species density and pH.

Other plants species are associated with depressed biological activity in the soil (Miles 1981), including classically, *C. vulgaris*. Table 1 shows a decrease in growth of test plants in soil from under *C. vulgaris* in an abandoned granite quarry, compared with that from under adjacent partly colonized ground and adjacent birch stands. One reason for this depression of growth might be an accumulation of lipids in the soil. Mor humus of heathland typically has about twice the lipid content of the mull humus of broad-leaved woodlands, and these lipids are generally inhibitory to soil micro-organisms and to plant growth (Stevenson 1966: Fustec-Mathon, Righi & Jambu 1975). Another reason might be the production of phytotoxic organic acids (Jalal & Read 1983a, b). Table 1 also shows that the effectively unweathered (the quarry was abandoned in 1938), coarse-sandy granite soil was surprisingly fertile compared with old birchwood soil, and even potting compost.

TABLE 1. Mean dry weights (log_{10} mg) of 10-week old plants of three species grown in soil from under three different kinds of vegetation on the floor of a disused granite quarry, from an old birchwood, and in potting compost

	Granite quarry soils from under:			Brown podzolic soils from 91-year-old *B. pendula* woodland	John Innes No. 2 potting compost	LSD at 5% level
	partly colonized ground	dominant *Calluna vulgaris*	26-year-old *Betula pendula* scrub			
Above-ground dry weights						
Luzula sylvatica (Hudson) Gaudin	1·06	0·57	1·59	0·96	1·42	0·35
Raphanus sativus L. 'French breakfast'	1·47	1·09	1·92	1·57	1·82	0·23
Rumex acetosa L.	1·31	0·43	1·46	1·44	1·64	0·67
Below-ground dry weights						
R. sativus L. 'French breakfast'	1·48	1·38	2·31	1·71	2·29	0·35

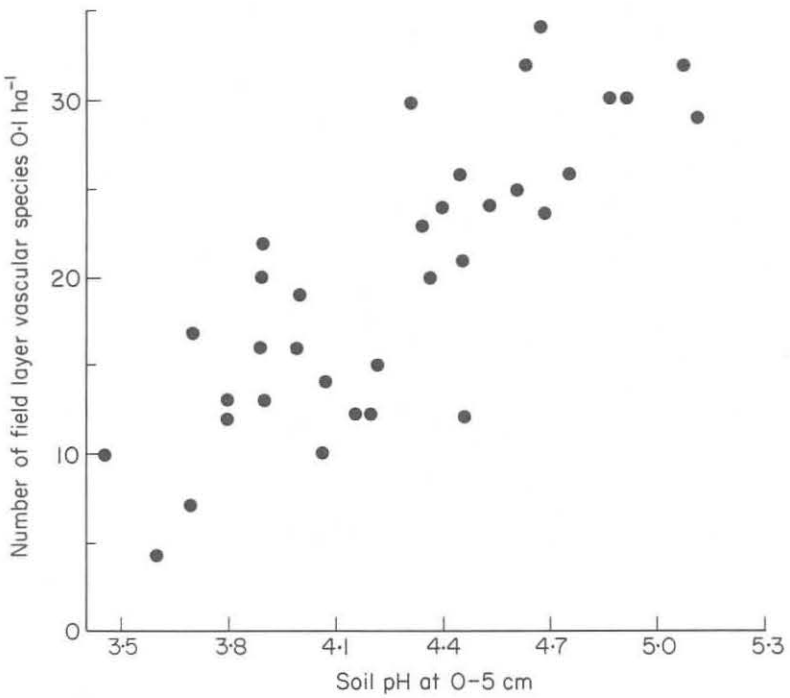

FIG. 6. Relationship between soil pH at 0–5 cm and the number of vascular plant species growing in the field layer of different aged, successional stands of *Betula pendula* and *B. pubescens* at twelve sites in Scotland and the north of England ($r = 0{\cdot}891$, $P < 0{\cdot}001$).

Natural granite soils in the region are now among the poorest in Scotland. This indicates how well plants may have grown as they colonized northwards after the last glaciation.

INTERACTIONS BETWEEN SOIL AND ABOVE-GROUND BIOTA

The seed bank

Persistent banks of dormant seeds (i.e. potential vegetation) seem to be ubiquitous in soil (Harper 1977; Grime 1979). However, little is known about the mechanisms controlling the size and life expectancy of buried seed populations. After dispersal, before seeds and fruits become intimately mixed into the soil, many are probably consumed by birds, small mammals and invertebrates (Janzen 1971). As they become incorporated into the soil by downwash, biological mixing, or simply being covered by litter, they are probably less readily found by predators, but quantities are probably still consumed by burrowing the soil-living animals. Earthworms, where present, ingest some seeds (Chippindale & Milton 1932; Milton 1939), and many do not survive passage through the gut (McRill & Sagar 1973; McRill 1974).

TABLE 2. 1978 seed rain, seed bank in July 1978, and estimated annual death rate k', of seeds of *Calluna vulgaris* in *C. vulgaris* dominated vegetation at varying altitudes in the Cairngorm Mountains (from Miller & Cummins 1981)

Altitude (m)	Mean annual rain of germinable seeds (10^3 m^{-2})	Numbers of buried germinable seeds (10^3 m^{-2})	Annual death rate, k'
370	420	69	0·86
580	53	68	0·44
860	0·24	14	0·02

Most buried seeds probably succumb to infection from microbial pathogens (Baker 1972). Despite the variety of likely fates, populations that are isolated from the seed rain decline in an approximately exponential manner (Roberts 1962, 1970; J. Miles, unpubl.), suggesting that the death risks are constant in time, independent of the age of the population.

Indirect evidence that the longevity of the seed bank depends on extrinsic factors is given in Table 2. It shows that the production of germinable seeds of *Calluna vulgaris* decreased dramatically with increasing altitude. At 860 m (which is near the altitudinal limit of growth of *C. vulgaris*) seed production was only 0·1% of that at 370 m. However, the seed bank (determined before the new seed crop, or at least most of it, was shed) did not diminish correspondingly. Estimated annual death rates (calculated as the loss coefficient, k', of Jenny, Gessel & Bingham 1949) were over forty times greater at 370 m than at 860 m. They suggest that one year's seed rain will disappear in 4–5 years at 370 m, but over centuries at 860 m. The lower death rates at higher altitudes are presumably mainly attributable to reduced predation and microbial infection, reflecting reduced biological activity in the soils with lower year-round temperatures. Part of the difference, however, could also be attributable to reduced catabolic rates within the seeds in a colder climate.

Seed dispersal by ants

As British ants nest in the soil (*sensu lato*), I class them here as part of the soil fauna. It has been known since the last century that ants transport seeds of many species, particularly of those that produce ant-attracting oil bodies or elaiosomes (Kerner 1891). Ant dispersal of seeds and fruits (myrmechochory) attracted considerable early attention (Uphof 1942), and Ulbrich (1939) thought it was common among woodland plants in parts of Germany. Interest in the subject waned post-war in the face of newer and more fashionable topics, but has been somewhat renewed of late. Berg (1975, 1981) has pointed out the enormous importance of myrmechochory in Australia; myrmecochorous species can constitute over half the flora in dry sclerophyll forest, and nearly half in heathland. Many dominant species of English lowland heath are collected and stored underground by *Tetramorium caespitum* (Brian, Hibble & Stradling 1965; Brian, Elmes & Kelley 1967). In

temperate North America, myrmecochorous species comprised 30–44% of the herbaceous flora in West Virginian forests (Beattie, Culver & Pudlo 1979; Beattie & Culver 1981), and 30% in beech–maple forest in New York State (Handel, Fisch & Schatz 1981). In the latter case, myrmecochorous species formed 40% of the above-ground herbaceous biomass, and over half of all herbaceous stems.

Apart from the advantages of dispersal, ant transport and often burial of seeds and fruits may benefit the plant by reducing seedling competition (Handel 1978) and securing seeds from predation (Culver & Beattie 1978; O'Dowd & Hay 1980), while elaiosome or aril removal may enhance germination (Horvitz 1981).

Logs and stumps as seedling niches

Niches allowing both seedling establishment and successful subsequent growth are commonly in short supply (Miles 1979). In north temperate forests, rotting tree stumps and logs allow saplings and herbaceous species to establish (Jones 1945; Franklin & Dyrness 1973). To see this is commonplace, and sometimes these substrates are almost the only places where saplings can be found. What changes

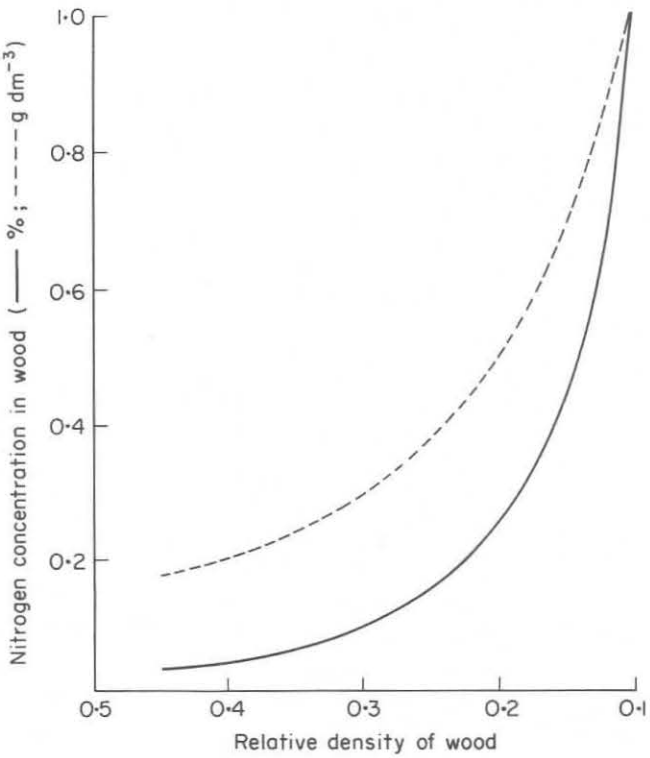

FIG. 7. Mean trend of accumulation of nitrogen in decomposing stumps of *Picea sitchensis*. Relative density is a measure of decomposition, freshly cut stumps being 0·4–0·5 g cm^{-2}, and stumps 10–20 years old, 0·1–0·15 g cm^{-2} (after Newell & Heal 1982).

TABLE 3. Density of seedlings and saplings of *Picea engelmannii* and *Abies lasiocarpa* regenerating on the trunks of fallen trees in varying states of decomposition in a *P. engelmannii – A. lasiocarpa* forest, Colorado (mean number 100 m^{-1} of log). (After McCullough 1948; decay classes following Triska & Cromack 1980.)

	Log decay class				
Plant height class	I Tree newly fallen	II Early decay visible; bark intact	III Bark sloughing; sapwood rotten, heartwood sound	IV Bark detached; heartwood rotten and crumbling	V More or less totally decomposed; log outline indistinct
< 30 cm	0	7	35	724	1974
> 30 cm	0	0	0	0	66

must occur in wood before seedlings can establish? I have found no answer in the literature. Certainly, seedlings only appear in quantity when the wood is well rotted (Table 3). I suggest that this may correspond to the phase of rapid accumulation of nitrogen shown by Newell & Heal (1982) (Fig. 7). This coincides with the level of nitrogen capital needed to sustain non-nitrogen fixing plants during primary succession (Bradshaw *et al.* 1982), i.e. about 70 mg dm^{-2}.

Root competition

Interest in root competition, as with myrmechochory, has unaccountably languished in recent years, although many early studies demonstrated the importance of tree root competition in controlling regeneration and the composition of the field layer (Miles 1979). Figure 8 shows the dramatic flowering response of *Anemone nemorosa* when plots in a mixed *Betula pendula–B. pubescens* wood were trenched to 0·5 and refilled. The effect was short-lived but made its point with me. Previously I had only seen such displays of flowering in *A. nemorosa* on roadside verges, and had attributed this to lack of shading.

Mycorrhizas

Mycorrhizas give considerable benefits. They help most plants to tap scarce nutrients, even utilizing soluble organic forms of nitrogen (Lundeberg 1970; Stribley & Read 1974; Bowen & Smith 1981). They accelerate stem maturation (Last *et al.* 1983), while sheathing mycorrhizas at least, protect roots from pathogenic fungi (Marx 1972; Sylvia 1983). The death of mycorrhizal hyphae may account for 80% of plant return to the soil of nitrogen, phosphorus and potassium (Fogel 1970; Fogel & Hunt 1983). Recent observations of sequences of fruit-bodies with time under a mixed *Betula pendula–B. pubescens* stand (Mason *et al.* 1982; Mason *et al.* 1983), coupled with laboratory studies (Deacon, Donaldson & Last 1983; Fox 1983), suggest that mycorrhizal successions may occur, with 'late stage' fungi being unable to form mycorrhizal associations with young plants in unsterile soils. Collections of

TABLE 4. Percentage composition in September 1977 of fruit-bodies of known or probable mycorrhizal fungi under different aged stands of birch (*Betula pendula* and *B. pubescens*) growing at four sites formerly under heather moorland: (a) *B. pendula* at Tulchan, near Advie, Morayshire; (b) *B. pendula* at Kerrow, near Cannich, Inverness-shire; (c) *B. pubescens* at Craggan, Strath Avon, Banffshire; (d) *B. pubescens* at Silpho, near Scalby, North Yorkshire

	(a) *B. pendula* aged (years)		
	21	41	93
Laccaria proxima	17		
L. laccata	6		
Lactarius rufus	5		
Leccinum versipellis	4		
Lactarius vietus	47	15	14
L. pubescens	7		29
Russula sp.	4	8	
Inocybe sp.		19	
Cortinarius sp.		15	
Lactarius tabidus		4	
Paxillus involutus		4	
Xerocomus chrysenteren		4	
Cantharellus cibarius		31	29
Amanita citrina			14
Russula foetens			14

	(b) *B. pendula* aged (years)		
	20	29	72
Boletus impolitus	3		
Russula atropurpurea	3		
Cortinarius spp.	78	18	
Lactarius pubescens	16	5	5
Hebeloma spp.		52	
Boletus edulis		3	
Tricholoma nudum		8	
Amanita muscaria		8	32
Leccinum scabrum		3	5
Russula aeruginea		3	5
Tricholoma columbetta			28
Laccaria amethystina			10
Lactarius tabidus			10
Inocybe sp.			5

	(c) *B. pubescens* aged (years)		
	21	30	56
Cortinarius tabularis	27		
Leccinum scabrum	5		
Cortinarius armillatus	22	64	
Lactarius pubescens	15	3	
L. rufus	7	3	
Laccaria laccata	24		23
Lactarius vietus		24	10
Russula sp.		6	14
Lactarius turpis			27
Cortinarius sp.			23
Paxillus involutus			3

	(d) *B. pubescens* aged (year)				
	15	38	48	63	50–100
Russula sp.	29				
Lactarius rufus	29		5	4	
L. vietus	13	80	10	77	45
Amanita fulva	29	3	28	4	
Paxillus involutus		3	24		3
Russula ochroleuca		5	33	7	45
Leccinum scabrum		6			3
Xerocomus subtomentosus		3			
Lactarius turpis				4	
Leccinum versipellis				4	
Russula atropurpurea					3

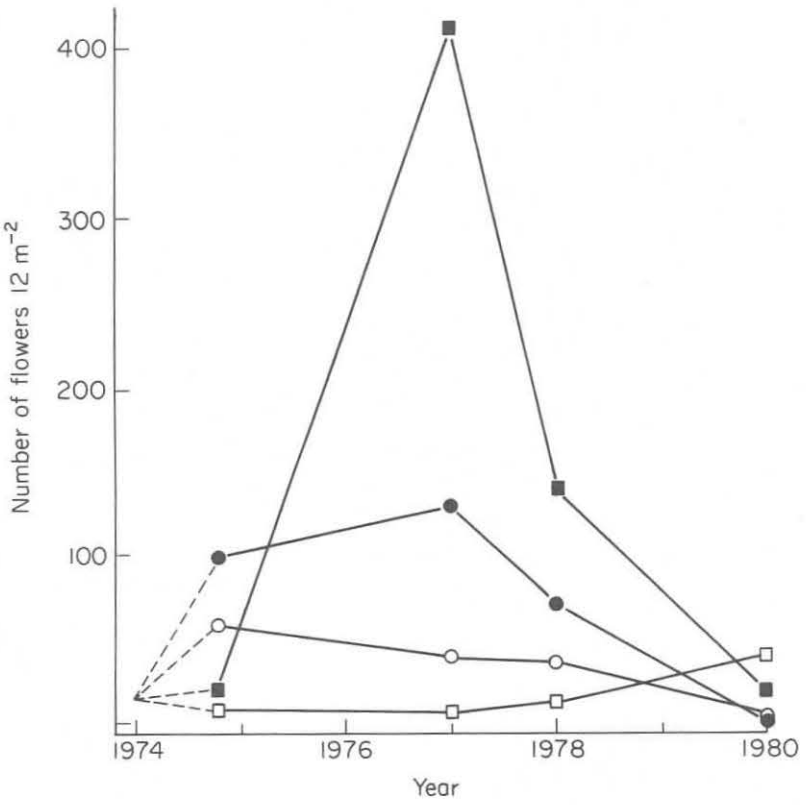

FIG. 8. Changes in flowering of *Anemone nemorosa* and *Oxalis acetosella* under a 30-year old mixed *Betula pendula–B. pubescens* wood at Hill of Brathens, Kincardineshire, after plots were root trenched to 0·5 m depth in February 1974, lined with polythene, and refilled (*A. nemorosa* trenched ■, untrenched □, *O. acetosella* trenched ●, untrenched ○).

fruit-bodies at four sites with successional sequences of *Betula* (Table 4) suggest that mycorrhizal successions, caused directly or indirectly by the ageing trees, are a widespread phenomenon. Their functional significance is, however, unknown.

Effects of herbivores

Invertebrate herbivores usually seem to consume only a small proportion of plant production. Their egesta are therefore, unlikely to be important sources of N and P. In contrast, vertebrate herbivores affect soil fertility directly by voiding faeces and urine (Wolton 1955; Peterson, Woodhouse & Lucus 1956; Lotero, Woodhouse & Peterson 1966), with consequent increases in herbage production (Wheeler 1958; Weeda 1967). This is an important mechanism promoting nitrogen and phosphorus cycling in poor upland soils in Britain (Floate 1972). During the survey of successional sequences of birch noted earlier, I gained the impression that the field layer had changed more rapidly where past grazing pressures seemed to have been

greater. Although this could not be quantified, it would tend to follow if dunging and urination had speeded up the cycling of nitrogen and phosphorus.

Other effects of herbivores may be more subtle. Several studies have shown that defoliation increases primary production (thus indirectly influencing soil processes) by increasing growth rates of remaining tissues (Scott, French & Leetham 1979), by delaying senescence (Jameson 1963), and by stimulating growth through the effects of saliva (Reardon, Leinweber & Merrill 1972). In the last case, the physiologically-active chemical seems to be thiamine (Reardon, Leinweber & Merrill 1974). A similar effect has been noted in grasshoppers (Dyer & Bokhari 1976). Equally subtle is the finding that small fungus-eating mammals seem to be the primary vectors of spore dissemination of mycorrhizal fungi that produce fruit-bodies below ground (Maser, Trappe & Nussbaum 1978).

EPILOGUE

The examples given indicate how varied and important are the interactions between soil and above-ground biota and biotic processes. As a concluding example of ecosystem complexity and connectedness, Fig. 9 shows that most of the major ecosystem components directly influence three parameters, variously touched upon earlier, that directly affect plant welfare:soil pH, phytoactive chemical production, and plant nutrient supply.

It is clear that most of the functional interactions of ecosystems are transient rather than fixed. Vegetation, the predominant primary producer in terrestrial

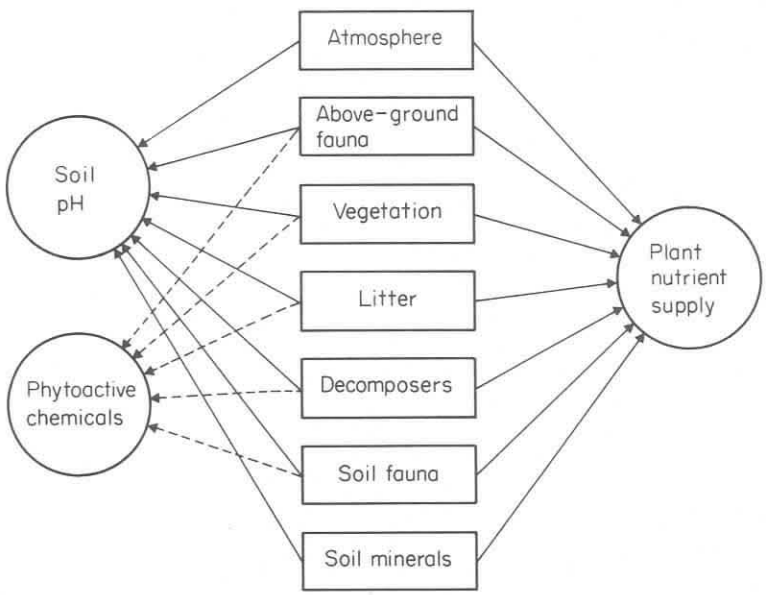

FIG. 9. Major ecosystem components influencing three parameters affecting plant welfare, soil pH, production of chemicals influencing plants, and plant nutrient supply.

ecosystems, varies continually in space and time. Even in apparently stable vegetation, episodic disturbances increasingly seem to be the rule rather than the exception. Long-term equilibria of plant-dependent soil processes are thus likely to be equally rare. As vegetation changes, the associated populations of consumers and decomposers tend to vary correspondingly, reflecting the changes in their environment in physical structure, micro-climate, plant and litter chemical composition (Burges & Raw 1967; Swift *et al.* 1979), and plant-induced soil changes (Miles 1981). An ecosystem thus has no absolute reality, other than as a concept. Any ecosystem must be defined arbitrarily, in an *ad hoc* manner. The ecosystem concept during the past two decades or so has been an invaluable peg on which to hang ecological process studies, in particular those of nutrient cycling and energy flow (Likens *et al.* 1977; Bormann & Likens 1979; Swift *et al.* 1979). However, the dynamic nature and extreme variability of soil properties must constantly be borne in mind by soil biologists and ecologists.

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